J. New York Entomol. Soc. 98(1):93–102, 1990

BIOLOGY AND IMMATURE STAGES OF *COENIA CURVICAUDA* (DIPTERA: EPHYDRIDAE)

B. A. Foote

Department of Biological Sciences, Kent State University,
Kent, Ohio 44242

Abstract.—Information is presented on the life cycle and larval feeding habits of *Coenia curvicauda* Meigen, a widely distributed and common species of the ephydrid subfamily Ephydrinae. The larvae are trophically generalized and are able to utilize a wide variety of algae as well as decomposing plant detritus. However, certain algal foods seemingly are more suitable, as they permit larval growth to be completed more quickly. In northeastern Ohio, the life cycle can be completed in 16–25 days, and there are 9–12 generations a year. The egg, mature larvae, and puparium are described and illustrated. The larval morphology is compared to that of *Paracoenia fumosalis* Cresson.

The genus *Coenia* Robineau-Desvoidy, a member of the subfamily Ephydrinae, is considered by Mathis (1979) to be relatively close phylogenetically to *Lamproscatella* Hendel, *Scatella* Robineau-Desvoidy, and certain other related genera within the tribe Scatellini but to be relatively distantly related to another scatelline genus, *Paracoenia* Gresson. This latter conclusion is in distinct contrast to earlier workers who tended to place *Coenia* close to *Paracoenia* (Wirth, 1965). In fact, Sturtevant and Wheeler (1954) considered *Paracoenia* to be a subgenus of *Coenia*. Wirth (1965) included *Coenia* in the tribe Scatellini, but Mathis (1979) has recently concluded that this tribe is paraphyletic and merely an assemblage of convenience.

Coenia includes few species that only occur in northern areas of the Holarctic Region. *Coenia palustris* (Fallén) is limited to Europe; *C. alpina* Mathis apparently is restricted to North America; whereas the third species, *C. curvicauda* (Meigen), has a Holarctic distribution (Mathis, 1975). In the Nearctic Region, *C. curvicauda* ranges from eastern Canada to Alaska and south to New Jersey, Ohio, Nebraska, and Montana (Mathis, 1975, map 3).

Nothing has been published on the life cycle, larval feeding habits, or morphology of the immature stages of any species of *Coenia* (the paper by Beyer, 1939, on *Cänia fumosa* Stenhammar actually deals with a European species of *Paracoenia*). The present paper outlines the life history; elucidates the larval feeding habits; and describes and illustrates the egg, third larval instar, and puparium of *C. curvicauda*.

MATERIALS AND METHODS

All observations were made between 1982 and 1988 in Portage County, Ohio near the city of Kent. Life-cycle information was obtained under laboratory conditions of a constant temperature (ca. 22°C) and a photoperiod of 16L:8D. To determine larval food preferences, monocultures of algae were established on nutrient agar in sterile petri dishes. Most of the algal cultures were obtained from The University of Texas Culture Collection of Algae. Species of algae utilized, and their UTEX strain numbers, are listed below. Species lacking strain number were obtained in nature or from the phycology laboratory at Kent State University. Feeding tests were performed as outlined in Zack and Foote (1978).

Cyanophyceae: *Anabaena flos-aquae* (1444), *Anabaena variabilis* (B377), *Calothrix* sp., *Cylindrospermum* sp. (LB942), *Gloeocapsa alpicola* (B589), *Lingbya spiralis* (B1831), *Oscillatoria tenuis* (B428), *Synechococcus leopoliensis* (625).

Chlorophyceae: *Chlamydomonas eugametos* (9), *Chlorococcum* sp., *Cosmarium botrytis* (175), *Scenedesmus quadricauda* (76).

Bacillariophyceae: *Navicula pelliculosa* (668).

Xanthophyceae: *Botrydiopsis alpina* (295).

LIFE HISTORY

Adults of *C. curvicauda* usually are found in open or partially shaded wetlands having noticeable accumulations of decaying organic material. Deonier (1964) collected adults from mud-shore and limnic-wrack habitats, and Scheiring and Foote (1974) found them to be abundant on muddy shores and common in the limnic-wrack habitat. The latter workers recorded adults between early April and early October, but noted that populations were much reduced in July and August. They found larvae in moist to wet substrates having high concentrations of organic matter. Apparently, *C. curvicauda* can also occur in coastal habitats, as adults have been taken in salt marshes and wrack beds (Dahl, 1959; Simpson, 1976). I found adults most abundantly in open wetlands having relatively little emergent vegetation, but having high levels of decaying organic matter within or covering the substrate. They were particularly common over foul-smelling mud along a small, shallow drainage ditch that carried the effluent of a small sewage treatment plant. Larvae were abundant in the sewage-impregnated mud bordering the ditch. Other species of Ephydridae commonly collected with *C. curvicauda* included *Paracoenia fumosalis* Cresson, *Scatella favillacea* Loew, *S. picea* (Walker), *S. stagnalis* (Fallén), *Ochthera tuberculata* Loew, *Pelina truncatula* Loew, *Parydra aquila* (Fallén), *P. quadrituberculata* Loew, *Dichaeta caudata* (Fallén), and *Discocerina obscurella* (Fallén).

The flight period in northeastern Ohio extended from early March (5 March) to mid-October (17 October), with a definite decline in adult populations during the summer months. Fall populations were somewhat larger than those of summer, but distinctly smaller than those encountered in May and early June. No direct information is available on overwintering habits, but the collection of adults, including gravid females, during early March suggests that overwintering occurs as imagines.

Deonier (1972) reported that guts of field-collected adults contained about equal amounts of diatoms and other algal groups. The gut of a female that I collected on 5 March 1983, near Kent, Ohio, contained mostly diatoms.

The longevity of adults obtained in the laboratory rearings ranged from 10 to 27 days ($\bar{x} = 18$, N = 12). Males usually died a few days before females. The premating period averaged 3 days (N = 5).

Mating was resource based (Alexander, 1975), as it always occurred at sites possessing food resources (algae) required by the female. There did not appear to be any distinctive courtship behavior, and mating seemingly involved little more than efforts by males to initiate copulation with any suitably sized fly species. No evidence of lekking or territorial behavior was observed, and mating activities generally resembled those described for *Scatophaga stercoraria* (L.) (Scathophagidae) by Parker (1970). Mating occurred immediately after a receptive female was encountered, males did not "ride" females between copulations (Foote, 1983), and each copulation lasted from about a minute to nearly five minutes. At least in the laboratory breeding chambers, females mated repeatedly with the original male or with a series of males over a period of several days. Oviposition generally began two or three days after the initial copulation and continued nearly throughout a female's life span.

A female that was collected on 5 March on a warm (temperature reached 20°C), partly sunny day contained partially developed eggs. One ovary possessed 11 ovarioles; the other, 12. The number of recognizable eggs per ovariole ranged from 8 to 11 and averaged 9. These results suggest that early spring females have a potential fecundity of at least 198 eggs (9 eggs/ovariole × 22 ovarioles). Females confined to laboratory breeding jars deposited between 95 and 147 eggs (N = 3). One field-collected female deposited between 0 and 30 eggs daily between 12 April and 28 April, when she died. Between 13 April and 19 April, she laid an average of 15.4 eggs daily (11–30 eggs/day), but her daily production dropped to 0–2 during the last 7 days of life. Interestingly, all eggs obtained in the laboratory rearings were surrounded and partially covered by liquified fecal material deposited by the ovipositing female.

In the laboratory, females placed eggs into a lawn composed of a mixed culture of algae that covered a nutrient agar substrate in petri dishes. Most eggs were oriented horizontally and only slightly imbedded in the algal growth. In all cases the nipple end of the egg, which probably acts as a plastron (Hinton, 1960), was exposed to air. Eggs were found in nature similarly positioned in algae that covered sediments that were enriched by sewage effluent. Other eggs were found in finely divided detritus derived from decomposing plant material. Apparently eggs must retain contact with atmospheric air, as several that were forcibly held under water in small petri dishes failed to hatch. The incubation period lasted 2 to 3 days, with most eggs hatching in 2 days (N = 30). Hatching occurred through an eclosion line that developed just below the protruding nipple on the micropylar end of the egg.

Newly hatched larvae did not move more than few mm away from the egg shells before embedding themselves into the sediments and initiating feeding movements. In general, larvae remained buried in the food substrate up to their posterior spiracles but were able to feed for short periods (up to a few minutes) while completely immersed and out of spiracular contact with the overlying air. However, larvae that were forcibly retained below the surface of sediments died within 24 hours. When touched, larvae quickly retracted the breathing tube into the sediments but within several seconds again renewed contact with the surface. Larvae did not actively burrow through the sediments but remained relatively immobile except for continuous probing movements by the anterior end. Feeding consisted of rapid forward and backward movements by the mouthparts, with the mouthhooks dragging the microbially-enriched sediments towards the oral opening located on the ventral side of the cephalic segment. The conspicuous comb-like structures on the facial mask (Fig. 11) undoubtedly also aided in moving food materials into the preoral cavity. The floor of the tentoropharyngeal sclerite possesses 9 Y-shaped ridges, with each ridge bearing apically a series of closely-spaced lamellae that collectively served as

Table 1. Results of larval feeding tests for *Coenia curvicauda* on different algal monocultures.

Algal species	Percent reaching different instars				
	n	2L	3L	P	A
Cyanophyceae					
Anabaena flos-aquae	10	100	100	70	70
Anabaena variabilis	10	40	30	30	10
Calothrix sp.	20	100	80	80	80
Cylindrospermum sp.	10	0	—	—	—
Gloeocapsa alpicola	10	0	—	—	—
Lingbya spiralis	20	40	20	15	0
Oscillatoria tenuis	20	80	70	55	55
Synechococcus leopoliensis	15	90	60	55	47
Chlorophyceae					
Chlamydomonas eugametos	10	100	100	60	60
Chlorococcum sp.	10	100	80	0	—
Cosmarium botrytis	10	20	0	—	—
Scenedesmus quadricauda	30	60	23	0	—
Bacillariophyceae					
Navicula pelliculosa	10	100	100	100	90
Xanthophyceae					
Botrydiopsis alpina	10	100	80	20	10

a filtering mechanism. This filter functioned to separate small particles from the semi-liquid medium that was drawn into the pharynx and concentrated the particles into a bolus that was subsequently passed backwards to the foregut (Dowding, 1967). Guts of field-collected larvae contained a wide assortment of detrital particles, algal cells, yeast colonies, fungal hyphae, and bacteria. Larvae were reared successfully in the laboratory on a diet of crushed, decaying lettuce as well as on monocultures and mixed cultures of microorganisms. Table 1 presents the results of exposing newly hatched larvae to 14 different algal monocultures. The data suggest that the larvae are rather non-selective feeders, as they were able to complete development and produce adults on 8 of the algal species tested. Another indication that the larvae are polyphagous is the fact that they were able to utilize rotting lettuce, mud rich in sewage, mixed yeast cultures, and a variety of decaying basidiomycete fungi, although they failed to develop on pure cultures of the bacterium *Escherichia coli* (Migula) Castellani and Chalmers and the yeast *Rhodotorula aurantiaca* (Saito) Lodder. Larvae probably are best characterized trophically as being relatively non-selective microphages.

Although larvae were able to complete development on 8 species of algae, the total developmental time (combined larval and pupal periods) varied considerably among the different algal substrates (Table 2). Thus, *Navicula pelliculosa* and *Anabaena variabilis* gave the shortest developmental times (16.0 and 17.0 days, respectively), whereas the combined larval and pupal period was distinctly lengthened when *Botrydiopsis alpina* served as the larval food (29.5 days).

Table 2. Developmental time in days for *Coenia curvicauda* reared on different algal monocultures.

Algal species	Larval period		Pupal period		Combined period	
	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
Anabaena flos-aquae (N = 7)	10.3	0.49	8.9	0.69	19.0	0.82
Anabaena variabilis (N = 1)	11.0	—	6.0	—	17.0	—
Calothrix sp. (N = 17)	8.5	1.33	9.6	0.79	18.1	1.07
Oscillatoria tenuis (N = 6)	8.0	0.63	10.3	0.82	18.3	1.03
Synechococcus leopoliensis (N = 3)	9.7	0.78	9.3	0.58	19.0	2.00
Chlamydomonas eugamatos (N = 6)	12.0	2.19	11.3	1.86	23.3	3.61
Navicula pelliculosa (N = 9)	8.9	0.78	7.1	0.78	16.0	1.12
Botrydiopsis alpina (N = 2)	18.0	0.00	11.5	0.71	29.5	0.71

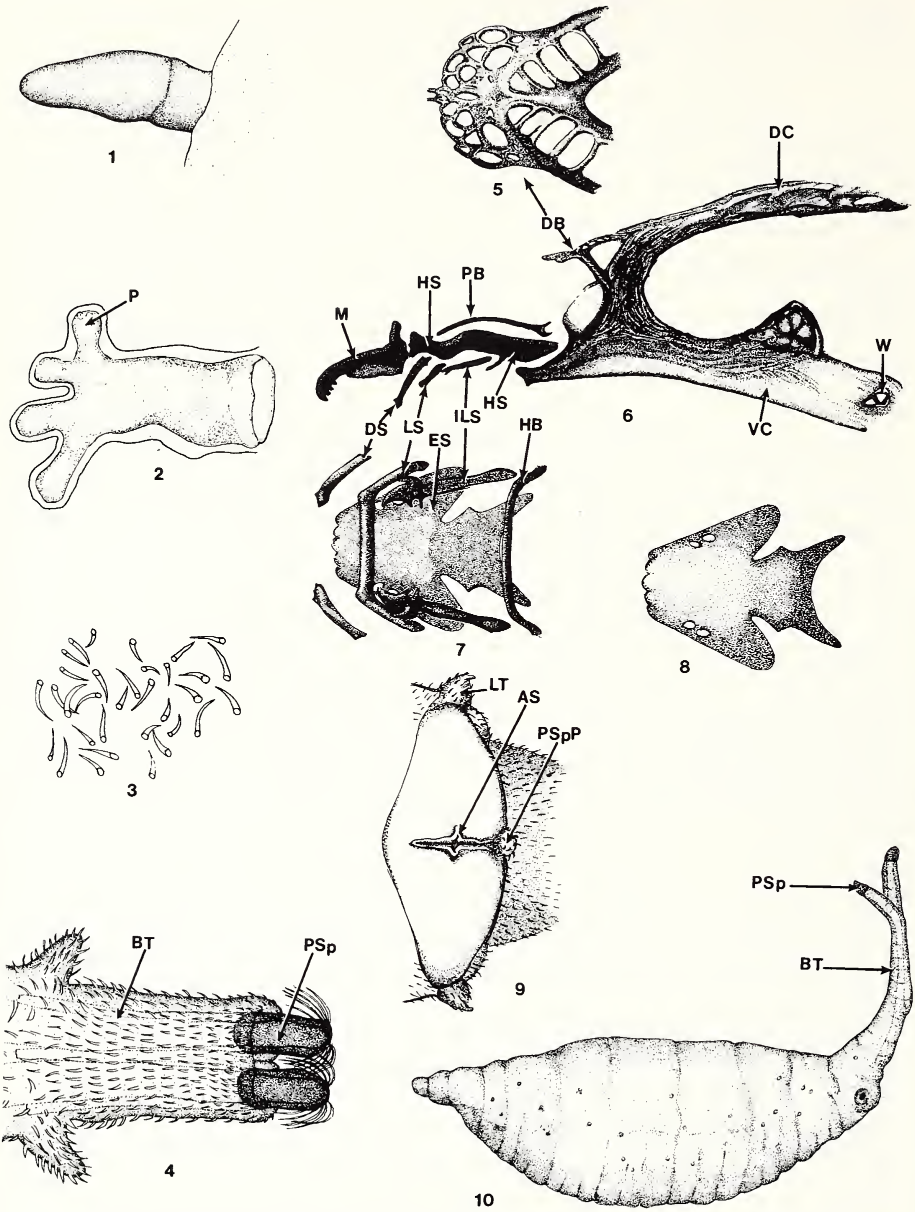
Mature larvae ceased feeding, emptied their gut contents, and increased their wandering activities prior to pupating. Many larvae moved to somewhat higher and possibly drier areas within the rearing dishes where they became relatively inactive and soon formed puparia. Other larvae crawled out of the dishes and eventually desiccated on the laboratory table. This behavior suggests that the larval microhabitat may not be the preferred site for pupation and that mature larvae move to somewhat drier areas before forming puparia.

When larvae were reared on *N. pelliculosa,* a diatom, the first larval stadium lasted an average of 1.7 days; the second, 1.7 days; and the third, 5.5 days (N = 9). The pupal period lasted 5–8 days and averaged 7 days (N = 5). The total developmental period from deposition of eggs to emergence of adults ranged between 14 and 20 days. This suggests that 9 to 12 generations could be produced during a warm season that in northern Ohio lasts from mid-April to mid-October (180 days).

DESCRIPTIONS OF IMMATURE STAGES

Egg. Length: 0.55–0.68 mm, $\bar{x}$ = 0.62 mm; width: 0.19–0.23 mm, $\bar{x}$ = 0.21 mm (N = 10). Elongate-ovoid, micropylar end with short, broad nipple arising on dorsal side; opposite end rounded. Chorion striated, ends of egg more reticulated. White.

Mature larva. Length: 7.2–8.0 mm, $\bar{x}$ = 7.6 mm; width: 1.3–1.6 mm, $\bar{x}$ = 1.4 mm (N = 5). Muscidiform, tapering anteriorly, caudal segment elongated to form retractile breathing tube; integument covered with fine pubescence of slightly darkened spinules, spinules uniform, none broadened to form dorsal patterns. Thoracic and abdominal segments bearing 2 kinds of sensilla; each rayed sensillum with slender tubular base and 4–5 elongate apical branches; each rosette sensillum short and peglike. Last two thoracic and first 7 abdominal segments each with 7 pairs of rayed sensilla: 1 dorsal, 2 dorsolateral, 1 lateral, 1 ventrolateral, and 2 ventral pairs; caudal segment with 6 pairs of sensilla: 3 ventral and 3 lateral along length of segment. Each body segment except caudal one also with 3 pairs of rosette sensilla: one pair adjacent to dorsal rayed sensilla, another pair next to dorsolateral rayed sensilla, and third pair adjacent to ventrolateral rayed sensilla; caudal segment with only 2 pairs of rosette sensilla, one pair adjacent to anteromost pair of ventral rayed sensilla, and second pair next to anteromost pair of lateral rayed sensilla.



Figs. 1–9. *Coenia curvicauda*, mature larva. 1. Antenna. 2. Anterior spiracle. 3. Integumentary spinules. 4. Dorsal view of posterior end. 5. Dorsal view of dorsal bridge of tentoropharyngeal sclerite. 6. Lateral view of cephalopharyngeal skeleton. 7. Ventral view of sclerites associated with hypopharyngeal sclerite. 8. Dorsal view of epipharyngeal sclerite. 9. Perianal pad. 10. Lateral view of puparium. ABBREVIATIONS: AS = anal slit; BT = breathing tube; DB = dorsal bridge; DC = dorsal cornu; DS = dental sclerite; ES = epipharyngeal sclerite; HB

Cephalic segment (Fig. 11) retractile, bilobed; each antennomaxillary lobe bearing antenna apicodorsally and circular sensory plate apicoventrally, antenna (Fig. 1) elongate and appearing 2-segmented, circular sensory plate consisting of incomplete ring enclosing 4–6 peg-like structures; facial mask (Fig. 11) with several rows of comb-like structures anterior of and lateral to preoral cavity, teeth of combs long and slender, directed posteriorly. Prothoracic segment spinulose, bearing anterior spiracles posterolaterally; each spiracle (Fig. 2) with slender, tubular base and 4–6 finger-like apical papillae. Thoracic segments encircled by fairly distinct bands of somewhat darkened spinules, lacking prolegs ventrally but with indication of creeping welt on metathoracic-first abdominal segmental boundary; abdominal segments rather uniformly spinulose (Fig. 3) and lacking distinct spinule bands, with ventral creeping welts at segmental boundaries; breathing tube of caudal segment (Fig. 4) with pair of pointed fleshy protuberances laterally at midlength, tube branched apically with each branch bearing deeply pigmented spiracles at tip; perianal pad (Figs. 9, 12) transversely elongate, tapered laterally, pad bordered posteriorly by spinule patch behind anal slit and laterally by pointed fleshy tubercle.

Posterior spiracles (Fig. 4) with 4 narrowly oval spiracular openings radiating out from ecdysial scar; 4 spiracular hairs present around margin of spiracular plate, hairs profusely branched dichotomously and arising on peritreme near outer border of each spiracular opening; ecydsial scar somewhat blackened, situation on inner side of spiracular plate.

Cephalopharyngeal skeleton (Fig. 6) mostly deeply pigmented. Tentoropharyngeal and hypopharyngeal sclerites separated; dorsal cornua slender, narrower than ventral cornua and connected anteriorly by fenestrated dorsal bridge (Fig. 5); ventral cornua with conspicuous dorsal lobe at midlength and small window apically; pharyngeal filtering mechanism present. Hypopharyngeal sclerite (Fig. 7) with 2 transverse bridges connecting lateral arms; parastomal bars slender, apparently fusing with epipharyngeal sclerite anteriorly; labial sclerites slender in lateral view, not fusing with each other apically. Mandibles deeply pigmented, relatively narrow; hook part slightly decurved and with 4–5 accessory teeth along ventral margin; basal part slightly broader than hook part and usually with elongate window near ventral border; dental sclerites rod-like in lateral view.

Puparium (Fig. 10). Length: 7.0–8.2 mm, $\bar{x}$ = 7.5 mm; width: 1.4–1.7 mm, $\bar{x}$ = 1.6 mm (N = 4). Posterior end narrowed and upturned to form distinct breathing tube. Integumentary structure as in mature larva.

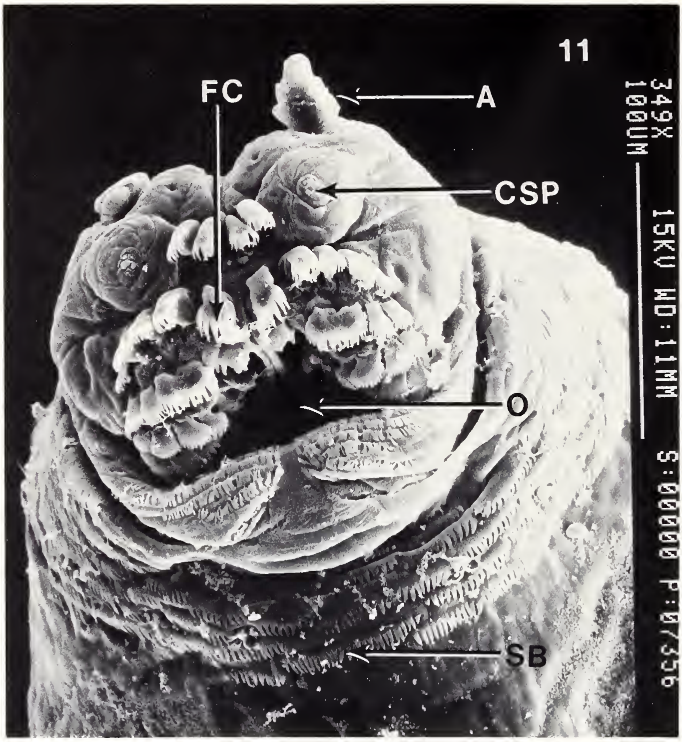
DISCUSSION

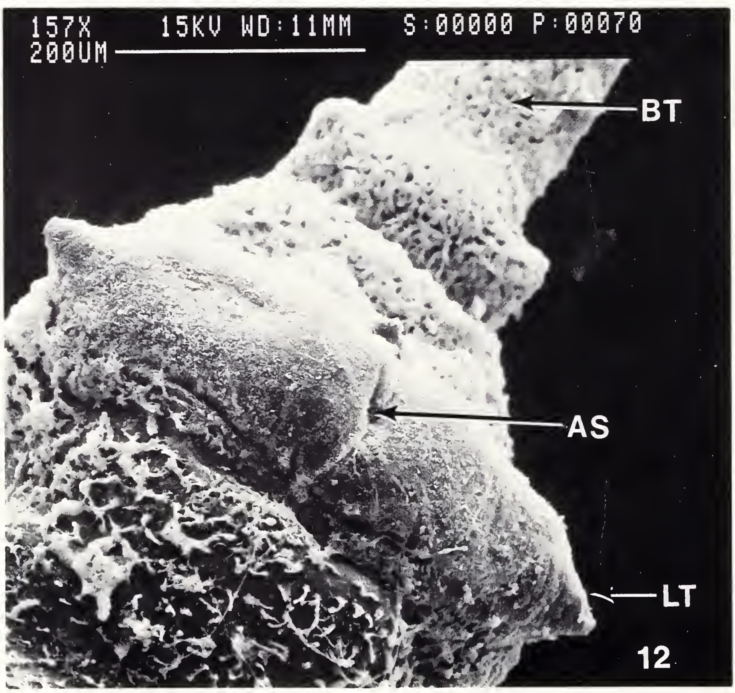
In the following section, the eggs, mature larvae, and puparia of *Coenia* are compared to those of *Paracoenia*.

Eggs of the two genera are distinctive and easily separated. Eggs of *Paracoenia*

←

= hypopharyngeal bridge; HS = hypopharyngeal sclerite; ILS = internal longitudinal sclerite; LS = labial sclerite; LT = lateral tubercle; M = mandible; P = papilla; PB = parastomal bar; PSp = posterior spiracle; PSP = postanal spinule patch; VC = ventral cornu; W = window.


11
FC
A
CSP
O
SB
349X
100UM
15KV WD:11MM S:00000 P:07356


157X 15KV WD:11MM S:00000 P:00070
200UM
BT
AS
LT
12

have a long, slender filament extended away from the micropylar end of the egg, whereas those of *Coenia* possess a short, nipple-like extension that is only slightly longer than broad.

The mature larvae of the two genera are also distinctive. Larvae of *Paracoenia* are considerably larger, averaging 9.0 mm from the anterior end to the base of the perianal pad; larvae of *Coenia* average only 5.8 mm in this dimension. Larvae of both genera have an elongate, retractile breathing tube that when extended is 5–8 times its basal width. The shape of the perianal pad is dramatically different in the two genera. In *Paracoenia* the pad is nearly circular. In *Coenia* the pad is transversely elongate, being somewhat wide medially and tapering laterally to a distinct tubercle. The anterior spiracles are also distinctive. In *Paracoenia* the spiracles are narrowly elongate and bear only 2–3 apical papillae, but in *Coenia* the anterior spiracles are somewhat hand-shaped and bear 4–5 papillae along the distal margin.

The puparia of the two genera are best distinguished by the distinctive shape of the perianal pad, as described in the larval characteristics.

LITERATURE CITED

Alexander, R. D. 1975. Natural selection and specialized chorusing behavior in acoustical insects. Pages 35–77 *in:* D. Pimentel (ed.), Insects, Science, and Society. Academic Press, New York.

Beyer, A. 1939. Morphologische, ökologische, und physiologische Studien an der Larven der Fliegen: *Ephydra riparia* Fallén, *E. micans* Haliday, und *Cänia fumosa* Stenhammer. Kiel. Meereforsch. 3:265–320.

Dahl, R. G. 1959. Studies on Scandinavian Ephydridae (Diptera Brachycera). Opuscula Entomol. Suppl. 15. 225 pp.

Deonier, D. L. 1964. Ecological observations on Iowa shoreflies (Diptera, Ephydridae). Proc. Iowa Acad. Sci. 71:496–510.

Deonier, D. L. 1972. Observations on mating, oviposition, and food habits of certain shore flies (Diptera: Ephydridae). Ohio J. Sci. 72:22–29.

Dowding, V. M. 1967. The function and ecological significance of the pharyngeal ridges occurring in the larvae of some cyclorraphous Diptera. Parasitology 57:371–388.

Foote, B. A. 1983. Biology and immature stages of *Nostima approximata*, a grazer of the blue-green algal genus *Oscillatoria* (Diptera: Ephydridae). Proc. Entomol. Soc. Wash. 85: 472–484.

Hinton, H. E. 1960. The structure and function of the respiratory horns of the eggs of some flies. Phil. Trans. Royal Soc. (B) 243:45–73.

Mathis, W. N. 1975. A systematic study of *Coenia* and *Paracoenia* (Diptera: Ephydridae). Gt. Basin Nat. 35:65–85.

Mathis, W. N. 1979. Ephydrinae (Diptera: Ephydridae)—a new perspective. Pages 47–60 *in:* D. L. Deonier (ed.), First Symposium on the Systematics and Ecology of Ephydridae (Diptera). N. Amer. Bethol. Soc.

Mathis, W. N. 1980. Studies of Ephydrinae (Diptera: Ephydridae), III. Revisions of some Neotropical genera and species. Smithson. Contr. Zool. 303:1–50.

←

Figs. 11, 12. *Coenia curvicauda*. 11. Facial mask. 12. Perianal pad. ABBREVIATIONS: A = antenna; AS = anal slit; BT = breathing tube; CSP = circular sensory plate; FC = facial comb; LT = lateral tubercle; O = oral opening; SB = spinule band.

Parker, G. A. 1970. The reproductive behavior and the nature of sexual selection in *Scatophaga stercoraria* L. (Diptera: Scatophagidae). IV. Epigamic recognition and competition between males for the possession of females. Behavior 37:114–139.

Scheiring, J. F. and B. A. Foote. 1974. Habitat distribution of the shore flies of northeastern Ohio (Diptera: Ephydridae). Ohio J. Sci. 73:152–166.

Simpson, K. W. 1976. Shore flies and brine flies (Diptera: Ephydridae). Pages 465–495 *in:* L. Cheng (ed.), Marine Insects. North-Holland Publ. Co., Amsterdam.

Sturtevant, A. H. and M. R. Wheeler. 1954. Synopses of Nearctic Ephydridae (Diptera). Trans. Amer. Entomol. Soc. 79:151–257.

Wirth, W. W. 1965. Family Ephydridae. Pages 734–759 *in:* A. Stone et al. (eds.), A Catalog of the Diptera of America North of Mexico. USDA. Agric. Handb. 276.

Zack, R. S., Jr. and B. A. Foote. 1978. Utilization of algal monocultures by larvae of *Scatella stagnalis.* Environ. Entomol. 71:509–511.

Received September 25, 1989; accepted October 30, 1989.